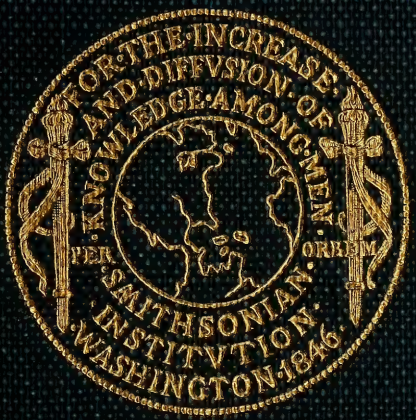
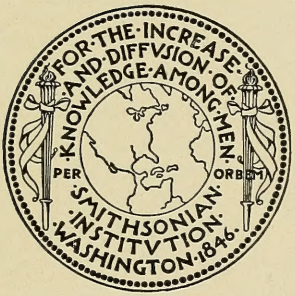


SMITHSONIAN LIBRARY

SMITHSONIAN INSTITUTION
WAR BACKGROUND STUDIES
NUMBER FIVE

THE NATURAL-HISTORY BACKGROUND OF CAMOUFLAGE

By
HERBERT FRIEDMANN



(PUBLICATION 3700)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
DECEMBER 11, 1942

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE NATURAL-HISTORY BACKGROUND OF CAMOUFLAGE

By HERBERT FRIEDMANN
Curator, Division of Birds, U. S. National Museum

(With 16 Plates)

INTRODUCTION

If we look up the word "camouflage" in a standard dictionary, we find it defined as concealment by disguise. The disguise may be of such a nature as actually to simulate the immediate background or merely to break up the outline or reduce the visible solidity of the object camouflaged. When man tries to camouflage an object, he is literally disguising it; in nature, on the other hand, the "disguise" is the normal coloration and is so termed because it has the effect, without effort, that man consciously aims for in his attempts. Although the word "camouflage" did not come into common usage until the time of the last war, the application by man of the ideas involved dates far back into antiquity. Based originally upon his observation of its occurrence in nature and its relative effectiveness under varying circumstances, it has been adapted by man to his own purposes. So far, these purposes have been chiefly related to warfare, although to a lesser extent in civilized societies and to a somewhat greater one in primitive peoples, camouflage has been applied to such activities as hunting and fishing as well.

The essential elements involved in camouflage are those of concealment and surprise. Concealment, to use military adjectives, may be either defensive or offensive (i.e., the value may be to render a prospective victim safe by its invisibility to a predaceous enemy, or it may render the marauder invisible from, and thereby help it to capture, its intended quarry). Most wild creatures live in constant danger from enemies or are themselves ever on the alert for prospective prey. They do not know the comparative peace and security of our peace-time civilized lives. It is, therefore, not surprising to find animals of all sorts exhibiting countless types and degrees and variations of such concealing adaptations as are implied by the term "camouflage." One of the fundamental factors in the lives of wild creatures is the combat between species (for food primarily, one feeding on the other or competing with it for a common food supply), generally referred to as the struggle for existence. The

problem of self-preservation in nature is very real, ever present, and often so difficult to cope with that some species appear to be numerically limited by it to a very marked degree. As has been emphasized recently by Cott (The Royal Engineer's Journal, vol. 52, p. 502, 1938), the vital,

> . . . urgent nature of this . . . problem of self-preservation is reflected in the variety and specialization of Nature's adaptive experiments in offence and defence. For instance, we see evidence for this in . . . speed, on land, in the air, and under water, by pursuer and pursued; in the use of stealth and surprise, of deception and ambush; in the display of warning signals, or of alluring baits; in the elaboration of smoke screens, traps, nets and parachutes; in retreat obtained by burrowing underground, or by the adoption of nocturnal habits; in the development of poison, and of deadly apparatus in the form of fangs or stings for its injection into the bodies of enemies or prey; in protection afforded by plated or spiny armor; and in the use of chemical warfare which is practised, for instance, by certain insects; and of poison gas, by creatures like the skunk.
>
> Of all these various adaptations—which it will be noted each have their parallel in the paraphernalia of modern warfare—perhaps none is so important, so widely distributed, or so perfect as that which renders animals inconspicuous, and often well-nigh invisible, in their natural surroundings.

He even goes so far as to say that

> . . . concealment appears to have been one of the main ends attained in the evolution of animals. And although in most spheres of modern warfare man has now (though in some cases only recently) advanced far ahead of the animal creation in his equipment for protection and aggression—in regard, for instance, to the development of armor and mobility, to the use of projectiles and of devices such as the balloon barrage (which in principle is a gigantic spider's web), smoke screens (which are used with effect by cuttle-fishes who dart for safety behind a dense cloud of sepia), and of instruments such as range-finders and sound-detectors and the like—the case of camouflage is an exceptional one.

During the last war camouflage was developed extensively along such lines as dazzle-painting of ships to break up their mass and render their outlines less definite and less recognizable, of splotch-painting of field artillery pieces to simulate their surroundings, and of lightening those parts of objects that were usually in shadow to reduce the visual solidity of the objects involved. On the whole it may be said that the bulk of the camouflage work done was to create concealment from ground level or at least from fairly low levels. Concealment from high above was relatively less important then than now. However, with the present enormous development in aerial warfare and the ever-increasing use of the air arm in both military and naval operations of all kinds, the problem of effective concealment has come to resolve itself more into concealment at a distance or from a height than from nearby. It is probably no exaggeration to say that military camouflage has a greater and more

vital importance now than it did in previous wars. Coincident with this increase in its use in warfare, there has been a growth of interest in the subject on the part of the public in general. Military camouflage, particularly with respect to its new developments and discoveries and applications, is necessarily a secret of the armed forces. But the natural-history basis of all this work may be here outlined for the interested reader.

The modern study of concealment and disguise in nature may be said to date from the work of the American artist-naturalist, Abbott H. Thayer. His first paper, originally published in an ornithological journal, The Auk, in 1896, was given wide distribution to scientific circles generally in the following year in the annual report of the Smithsonian Institution. First among our scientific institutions to recognize the theoretical and potential significance of this work, the Smithsonian has ever since followed with critical interest the unfolding of the subject. In 1909 Thayer brought together in definitive form his discoveries, ideas, and observations in a stimulating book entitled, "Concealing Coloration in the Animal Kingdom," which has served as a basis for all subsequent work and which is still useful and interesting in spite of subsequent data. Parts of it have been modified or even negatived by more recent studies, but on the whole it still serves as a good introduction to the subject. The most recent comprehensive book on the topic is Cott's "Adaptive Coloration in Animals," published in 1940. This book has very extensive literature references and may be consulted by the reader interested in details beyond the scope of a general paper such as the present one.

As Thayer first pointed out, in order to discuss intelligently the importance of distinguishability (i.e., the degree of possibility of being seen) in the lives of animals, we must remember that it is at the crucial moments when they are on the verge of catching or of being caught, that sight is commonly the indispensable sense. Smell and hearing may lead an animal toward its prey or away from its enemy, but in the last all-important seconds, sight is relied on almost entirely in many animals. It is for these moments that animals have most need of concealing coloration, and for which, on the whole, their coloration is often best adapted, and when looked at from the point of view of the potential victim or the potential enemy, as the case may be, often proves to be what Thayer terms "obliterative." It should be stressed at the outset that not all animals are concealingly colored, but this does not affect the interest in, and suggestive value of, those cases where they are. Overzealous students of animal coloration, especially the pioneers, have at times overstated their exposition of the subject by applying their ideas too widely

and by insisting too much on one general explanation to cover all cases. The fact that the camouflaging of animals is not successful at times is not entirely a negation of the camouflaging effect of their coloration, but may be due to the fact that other senses, such as smell, are not affected by the visual results of concealing coloration, and offset or render futile the best that camouflage can do.

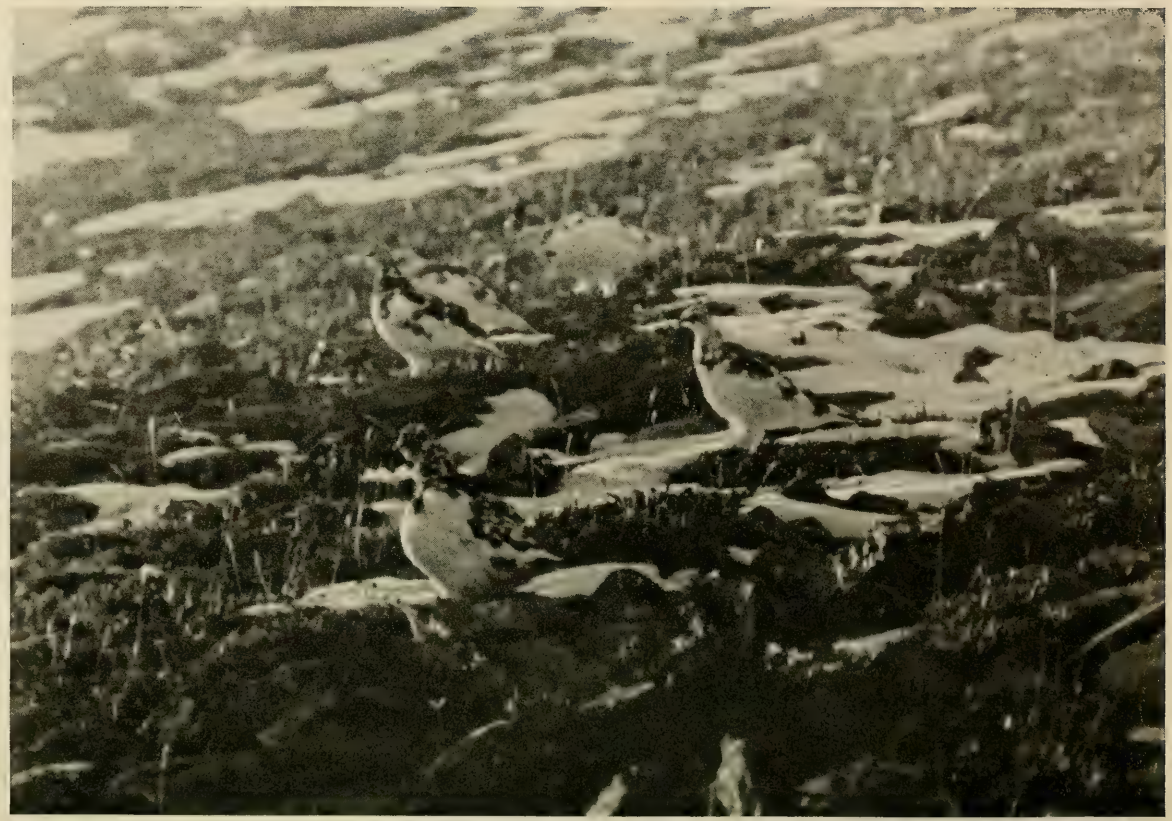
OBLITERATIVE SHADING

The immediate surroundings in which animals are found are naturally very variable in such matters as vegetation, amount of light, type of earth (whether rocks, gravel, sand, or bare earth are visible, or if everything is covered by leafage), and consequently the patterns needed for effective concealment are equally diverse. There is, however, one underlying factor common to animals in all of these backgrounds to a greater or lesser extent. It is this: Regardless of its particular color pattern, to become relatively invisible an animal must lose its appearance of solidity, or, to put it in other words, must not apparently cast a shadow on itself. The light falling on an animal usually comes from one direction, generally from above, so that some parts of the animal (usually its back) are in stronger light and the opposite parts (usually the underside) are in dimmer light or even in the shadow of the illuminated parts and tend to look darker. This is easily seen by placing a white ball on a table with the light coming from above—the under surface of the ball is shaded and at once reveals the spherical solidity of the ball, even though it be placed on a white table. In most animals the light and dark tones are so arranged that they somewhat counteract the effect of self-shadowing. This is brought about by having the darker tones where the light strikes (usually from above) and the paler tones on the parts in shadow (usually the lower parts). In other words, darker tones plus more light on one side tends to equalize paler tones plus shadow on the other. The result is a greater or lesser degree of reduction of the visible solidity of the animal. This distribution of light and dark tones on the animal, tending to counterbalance the unequal lighting the parts receive, is known as obliterative shading or countershading.

Countershading is, therefore, a basic principle of animal coloration and is of wide occurrence in nature. Many and quite unrelated groups of animals—mammals, birds, reptiles, fishes, etc.—in all parts of the world show it. Countershading may be described in relation to body form, to environment, and to habits. In some fishes with deep-bodied, laterally compressed forms having nearly vertical sides with but very slight convex curvature, strong countershading would defeat its own end, and it

ZEBRAS AND OSTRICHES IN THE EAST AFRICAN PLAINS

Note how the more distant zebras tend to blend into the background, the stripes becoming less and less distinct. (Photograph by C. E. Akeley, courtesy of American Museum of Natural History.)



ROCK PTARMIGAN AT MOUNT MCKINLEY NATIONAL PARK, ALASKA, SHOWING HOW WELL THE COLOR PATTERN OF THE BIRDS BLENDS WITH THAT OF THE BACKGROUND

(From Bull. 162, U. S. National Museum.)

1. COUNTERSHADING AND COLOR RESEMBLANCE IN THE SANDERLING (CROCETHIA ALBA)
(Drawn by W. A. Weber.)

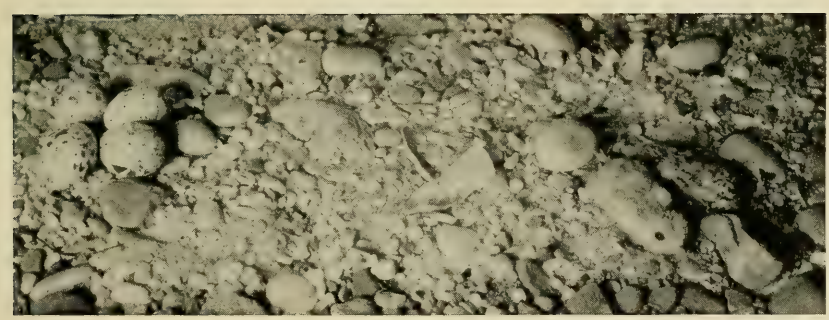
2. COLOR RESEMBLANCE WITHOUT COUNTERSHADING IS NOT ENOUGH
The white-tailed ptarmigan is revealed by its visual solidity and by its shadow.
(Drawn by W. A. Weber.)

1. Photograph from life.

2. Bird retouched to remove color pattern.

THE OBLITERATING EFFECT OF COLOR RESEMBLANCE IN THE WHITE-TAILED PTARMIGAN (LAGOPUS LEUCURUS)

1. Nighthawk, adult, young, and eggs.



2. Spotted sandpiper, young, and eggs.

CONCEALMENT AFFORDED BY COLOR RESEMBLANCE AND LOW SQUATTING POSITION

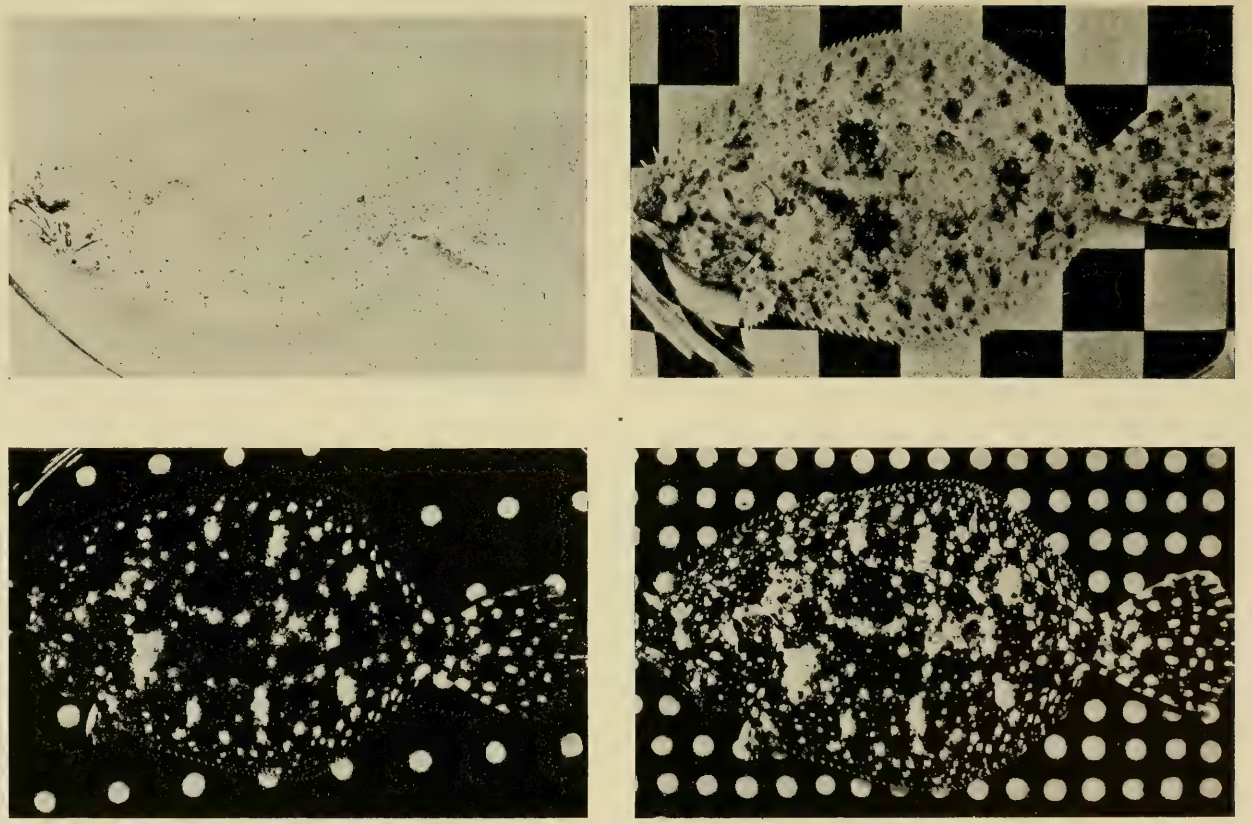
(From exhibits in the U. S. National Museum.)

1. SCORPION FISH (SCORPAENA PLUMIERI)

A good example of background resemblance both in color and in pattern. (From Longley and Hildebrand, Carnegie Inst. Publ. 535, 1941.)

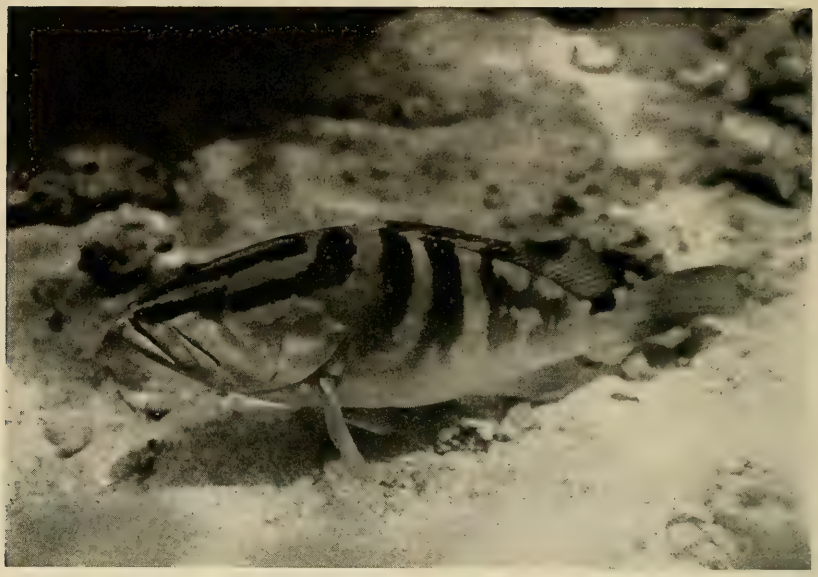
2. PARROT FISH (SPARISOMA PACHYCEPHALUM) IN FOREGROUND AT RIGHT

An example of blending with the background. (From Longley and Hildebrand, Carnegie Inst. Publ. 535, 1941.)



CHANGE IN COLOR AND PATTERN IN FLOUNDERS

These photographs are all of the same individual fish in an aquarium tank under which different card bottoms were placed. (From Mast, Bull. U. S. Bur. Fisheries, 1941.)



1. Swimming fish with "normal" coloration.

2. Resting fish changing its pattern to simulate surroundings.

NASSAU GROUPER (EPINEPHELUS STRIATUS), A FISH THAT ALTERS ITS COLORATION IN KEEPING WITH ITS BACKGROUND WHEN AT REST

(Photographs by Longley and Hildebrand.)

is noteworthy that such species are only slightly countershaded. In them, the degree of countershading shows a relation to the body form. (Examples are some of the ilarchid, scatophagid, and cichlid fishes, which, unfortunately, have no common names.) Other animals living in dim light, where shading would be less extreme, reveal in the slightness of their countershading a relation to this environmental factor. Likewise, animals living on open plains in bright sunlight, such as many antelopes, deer, larks, etc., are strongly countershaded. In the case of the shark sucker, a fish that has the habit of attaching itself by a sucker on its head to different parts of sharks, no countershading is present. However, since it may have any side uppermost, the lack of countershading may be considered in relation to this habit, as the fish maintains no constant position with reference to the source of light. In some caterpillars, the normal resting position is inverted; i.e., the back is down and belly up (example, the larva of the eyed hawk-moth, *Smerinthus ocellatus*), and it is indeed suggestive that in these creatures the countershading is reversed, being darker on the underparts and paler on the back.

The simplest form of countershading is merely an even, gradual transition from darkest on the parts receiving the most light to lightest on the parts most in shade. However, the same effect may, and in nature often is, effected by patterns which blend at rather short distance. For example, the spots in many spotted animals are larger on the back and become smaller on the sides and disappear on the underparts. If these spots are fairly close together, at a distance they tend to blend, forming a graded countershading. The body stripes of zebras, for example, are very broad on the back and taper very appreciably on the sides, giving again something of the effect of countershading. Mottram (Proc. Zool. Soc. London, 1915, pp. 679-692) expounded this idea that certain patterns found on animals become blended with distance and result in obliterative shading. This depends on the fact that if a pattern composed of alternating dark and pale markings, regardless of shape (they may be bars, stripes, spots, etc.), is looked at from successively increasing distances, a point will be reached from which the separate markings are lost in a blended effect, producing a tone depending on the relative amounts of dark and pale. It may be pointed out that this type of countershading is effective only at a distance and would be of little value to an animal in the last crucial seconds when it is about to catch or to be caught, but it might help prevent the situation from arising. However, the picture is not as simple as it has been presented so far in this paper. In the majority of cases, the immediate background against which even the most perfectly countershaded animal is to become invisible is not an even tone of one color

without breaks of any kind. If there is a background of grass, for example, each blade (when close up) has a shadow, or at least an outline; fallen twigs or leaves present even more shapes and irregularities of light and dark. The combination of countershading and pattern resemblance does result, however, in something similar to blended patterns, but, however, functions also, and in many instances chiefly, at close range. Having now grasped the role played by obliterative shading, we may proceed to examine the varieties of patterns and color arrangements found in animals which are concealingly colored.

COLOR RESEMBLANCE

Most of us have at one time or another become aware of a general similarity in appearance between certain animals and their surroundings. We have come to expect creatures living in deserts or sandy places to have pale or sandy hues and not to startle us with the brilliant greens and reds of some of the denizens of dense tropical forests. Without asking ourselves why or even consciously wondering, we connect the white of the polar bear and of the snowy owl with the snow and ice of their arctic habitat. Again it must be emphasized that not all animals are colored to resemble part of their environments; but the fact that exceptions are easy to find should not minimize the other fact that a very great many animals of all groups and living in all parts of the world and in all kinds of surroundings do bear on their coats a resemblance to their immediate environment.

General color resemblance, of necessarily only moderate value in effecting concealment, is shown by the preponderance of green birds, green tree toads, tree snakes, arboreal insects, etc., in the forested parts of the world, with a similarly large number of brownish forms dwelling on or in the forest floor. The common salt-and-pepper mottling or grayish-brown washes of shore birds show a general resemblance to their sandy or pebbly habitat. The whole question of color resemblance is still unfortunately largely couched in terms of human color vision. This will have to be altered with increasing knowledge of the color vision of the enemies of each animal showing color resemblance to its background. An example may help clarify this point. It is known that modern developments in infrared photography have revealed that different green animals differ greatly in their absorption of infrared light, and consequently those with great absorptive properties photograph as dark objects and those that reflect (and do not absorb) the infrared come out as light objects in the photographs. It is suspected that some

predaceous animals, such as certain owls, have a visual range beyond the human one on the infrared end of the spectrum. It would follow from this that some green animals might be seen readily by the owls while others would not, although to our eyes both would seem equally well concealed by their color. This problem is well known to the military camouflage experts in their experiments in concealing buildings, etc., with green paint or with leafy branches, the paint absorbing the infrared light and the chlorophyll in the leaves reflecting it.

Just as we may consider the general applicability of color resemblance in animals by virtue of the impressively large numbers of species that show some general color similarity to their surroundings, we may also sense its importance by considering the diversity of coloration in related species with diverse habits and habitats. Not only may we say that many forest denizens are greenish, many terrestrial dwellers brownish, many beach forms sandy in color, but also that within single groups of animals with diverse habitats we find all types of coloration in greater or lesser harmony with their backgrounds. In spiders, for example, the bark-dwelling species are usually brownish, those that live on stones are frequently grayish or with a broken pattern of dark and light; grass spiders are often green, while flower-inhabiting forms are whitish, yellow, pink, etc., in keeping with the flowers in each case.

Going still further, we find that color resemblance to particular local backgrounds varies geographically within single species. For example, in northern Africa crested larks of the genus *Ammomanes,* birds that dwell on the ground in open arid places, match surprisingly the color of the earth and sand. In one spot the ground color may be pale and tawny; so are the larks in that place. In another area, the terrain may be dark brown—so are the larks; in still another where blackish lava is a prominent feature of the substrate, the larks are similarly blackish. Yet all are one species, and intergrading specimens may be obtained between all their various extremes of color. A similar condition has been demonstrated in numbers of small mammals, such as deer mice, pocket mice, etc., by Benson (Concealing Coloration among some Desert Rodents of the Southwestern United States, Univ. California Publ. Zool., vol. 40, p. 1-70, 1933). The cases of this kind could be greatly multiplied, and practically every group of animals would be found to contain instances of the sort.

In some animals we find a seasonal change in coloration which appears to be directly correlated with seasonal changes in the background. Well-known examples of this type are many of the ptarmigan, a group of northern grouse which are mottled gray, brown, and black in the summer, blending remarkably well with their pebbly and grassy habitat, and

pure white in winter when their environment is covered with snow. The arctic fox shows a similar seasonal change in color. This type of color resemblance is, however, not very frequent in nature. In many cases the seasonal changes in coloration are not such as make for greater concealment.

All the examples of color resemblance hitherto mentioned are fixed for their durations, whether they be for life or for a season only. There are a number of types of color resemblance in animals which are variable and depend on changing environmental conditions. Some are built up gradually over a considerable period of time while others are very rapidly brought about. In a sense the seasonal changes already alluded to are a connecting type of color resemblance between definitely fixed and purely variable resemblances, but their period of effectiveness is long enough to warrant our considering them with the fixed types. In the lives of many kinds of animals, especially the more active ones (that is, not sessile or parasitic forms), individuals are constantly coming into contact with differing variations of their immediate surroundings. In many cases when danger is sensed these creatures tend to get back as rapidly as they can to their optimum backgrounds, but others have the ability to meet the changed conditions with variable coloration. Probably the best known case of rapid change in color is that of the chameleon, a small lizard which in the course of a few minutes can change its color through a surprising range of browns, reds, and greens, and darks and lights. Other lizards, such as some iguanas and geckos, are also known to possess the ability to alter their color rapidly. All are essential arboreal dwellers and rely on concealment more than on speed for their safety. Terrestrial forms rely, in most cases, on speed first, and then on concealment.

Fishes also possess amazing ability to change their color in keeping with changes in the background against which they find themselves. A notable series of experiments on the flounder was conducted by Mast (Changes in shape, color, and pattern in fishes and their bearing on the problems of adaptation and behavior, with special reference to the flounders, *Paralichthys* and *Ancylopsetta.* Bull. U. S. Bur. Fisheries, vol. 34, pp. 173-238, 1916). The flounders, ordinarily grayish brown or grayish olive in color, speckled with darker brown, not only can and do respond to altered backgrounds by changing from pale sandy yellow to dark blackish brown, but even alter the fineness or coarseness of their pattern in keeping with that of the background, simulating to an astonishing degree the texture and pattern of the bottom on which they are resting. When lying on a uniform muddy background, they tend to be uniformly colored, the speckling being much reduced in size and number of pecks

and in any difference in color from that of the rest of the fish; when placed on coarse gravel they become coarsely flecked and speckled. The mechanism by which the chromatophores in the skin are caused to effectuate the resulting changes is only partly understood, and is out of our province in this short review, our interest in the present paper being in what happens rather than in how it is caused. Longley found that reef fishes effect rapid color adjustments following vertical movements—some species change from the decidedly patterned colors that they wear when on the bottom (and can be seen only from above) to a uniform coloration when rising upward through deep water (where a bottom-approximating pattern would be revealing rather than concealing). Another important result of Longley's work is the demonstration that particular phases of color pattern are frequently correlated with definite types of activity in a manner which is in keeping with what seems to result in optical illusion (Year Book Carnegie Inst. Washington, vol. 27, pp. 158-163, 1918). For example, different fishes which have

> . . . alternate costumes of longitudinal stripes or uniform color, and of transverse bars, wear the former when in motion (an arrangement which makes for concealment in that it tends to mask forward movement) and the latter when at rest (when bars better serve to break up the contour and surface form against a broken background). Moreover, precisely similar adjustments are found in certain squids, which wear stripes for swimming and bands for resting [ex. Cott, Adaptive Coloration in Animals, p. 28, 1940].

Other examples of rapid color change have been recorded for other groups of animals—crustaceans, cephalopods, etc., but the important fact in the present connection is that beneath all the diversity of anatomical and physiological mechanisms involved in these different animals there is usually a common type of external stimulus (change in immediate environment as far as color, texture, etc., is concerned) and a common type of response.

Slower responses of similar type are known in certain insects and spiders. Poulton (Philos. Trans. Roy. Soc. London, vol. 178, pp. 311-441, 1887) showed by experimental studies that the larvae and pupae of certain butterflies possess the power of acquiring the coloration of their immediate surroundings, and showed that in species of *Vanessa* and *Pieris* the pupal adjustment was due to extreme sensibility of the larvae to reflected light during the final resting position prior to pupation.

Aside from obliterative shading and color resemblance many animals are still further concealed by the fact that the patterns of their coloration tend to break up their outlines, so that at a distance they seem to be

bits of the general surroundings rather than a recognizable shape which would tend to reveal them. This type of marking is known as—

DISRUPTIVE COLORATION

Even with better than average color resemblance and with some countershading, an animal is recognizable frequently by the fact that it presents a continuity of surface enclosed by an easily identified contour with which we (or its enemies) are ordinarily familiar. Thus, as Cott rightly insists,

> . . . for effective concealment, it is essential that the tell-tale appearance of form should be destroyed. The difficulty of doing this is met, often with extraordinary success, by the application of optical principles involving the use of pattern.

The function of disruptive coloration (which is a combination of color and pattern tending to break up or to reduce the visible outline of the animal) is to prevent or to delay the quick recognition of the object by sight.

> Its success depends not only upon optical principles, but upon a psychological factor. When the surface of a fish . . . is covered with irregular patches of contrasted colours and tones, these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them. The patterns themselves may be conspicuous enough, but since they contradict the form on which they are superimposed, they concentrate attention upon themselves, and pass for part of the general environment.

In a general way it may be said that the concealing effect of a disruptive pattern is greater if parts of its included pattern bear a good color resemblance to the background while other elements are strikingly distinct. The result is that the background seems to be seen through the animal in places, thus breaking up its visual form. Thus, a butterfly with a brown and green pattern would stand out as a butterfly against a background not containing either of these colors, but against a brown ground it would look like an aggregate of green spots, or, against a green ground, like a bunch of brown marks. This partial matching of the background is spoken of as differential blending. The effectiveness of this disruptive coloration is greatly increased if the adjacent contrastingly colored markings are also contrasting in tone (lightness or darkness). Cases such as the black collar bands on white or pale sandy plovers, of dark lateral longitudinal stripes on some pale-colored antelopes, come readily to mind in this connection. Everyone who has watched ring-necked plovers on the beach is aware of the disruptive effect of the collar at a significantly short distance.

CONSTRUCTIVE SHADING

The amount of difference in tone and color of immediately adjacent parts of the pattern has an important bearing not only on the degree of

success in its disruptive illusion, but also on the illusory pictorial relief it may create on the animal's surface. For example, if between the darkest and the lightest elements in a color pattern there is a gradual change from one to the other, the optical effect is that of a rounded surface (from shade to light); if, however, the darkest and the lightest elements are in immediate juxtaposition the effect produced is one of sharp ridges. Convexities may be made to appear concave, flat surfaces to assume undulations, and curved areas to flatten out, by the relation of adjacent pattern elements. The consequent distortion of the true shape of the creature into the resulting optical shape helps to conceal it just as well as the actual disruptive marks tend to reduce it to a mass of unconnected pieces. It is a curious fact, and one which demonstrates the enormous range of form, color, and pattern to be observed in animal coloration, that the general result of camouflaged appearance can be arrived at by such diametrically opposed methods as obliterative shading (which reduces or dissolves solid form) and constructive shading (which builds up the appearance of form that is not there—such as ridges, convexities, etc.). It may be well to state again, in different words, this matter of constructive shading and disruptive marks. In a very general way it may be said that the illusion of discontinuity (the result of disruptive marks in their simplest form) is a matter of color contrast on a fairly even surface, while constructive shading produces the illusion of surface modeling. A combination of the two not only fragments a whole into optically distinct and apparently unrelated parts, but also by its sculptural illusion renders it more difficult for the eye to conceive these pieces as being in the same plane and therefore connectable. In some instances constructive shading brings about an astonishing similarity to other objects such as the appearance of leaf vein ridges in some caterpillars.

Somewhat akin to constructive shading in its power of optical distortion is another type of disruptive pattern which has the effect of seeming to connect wholly distinct and not even adjacent parts of the body, thus further confusing the eye of the beholder and to that extent helping to hinder or delay recognition of the animal. A good example is the banded pattern in many frogs. When the frog is at rest (and in most cases no camouflage is of use when the creature is moving) the legs are folded close against the body and the bands of the body appear to be continuous with those of both the upper and the lower portions of the leg, optically merging them into one mass. If the bands went in different directions on the legs they would stand out distinctly from the body and attract attention.

In many fishes there is a dark diagonal disruptive band on the body which often extends on to the pectoral or the pelvic fins, which, if not

so connected by pattern with the body would be much more noticeable. Many insects show similar patterns involving legs or antennae as well as portions of the body. This type of color pattern has been termed coincident disruptive pattern by Cott, who was the first to emphasize the continuity of patterns of the head across the eye in order to hide the eye itself, ordinarily the most difficult part of an animal to conceal.

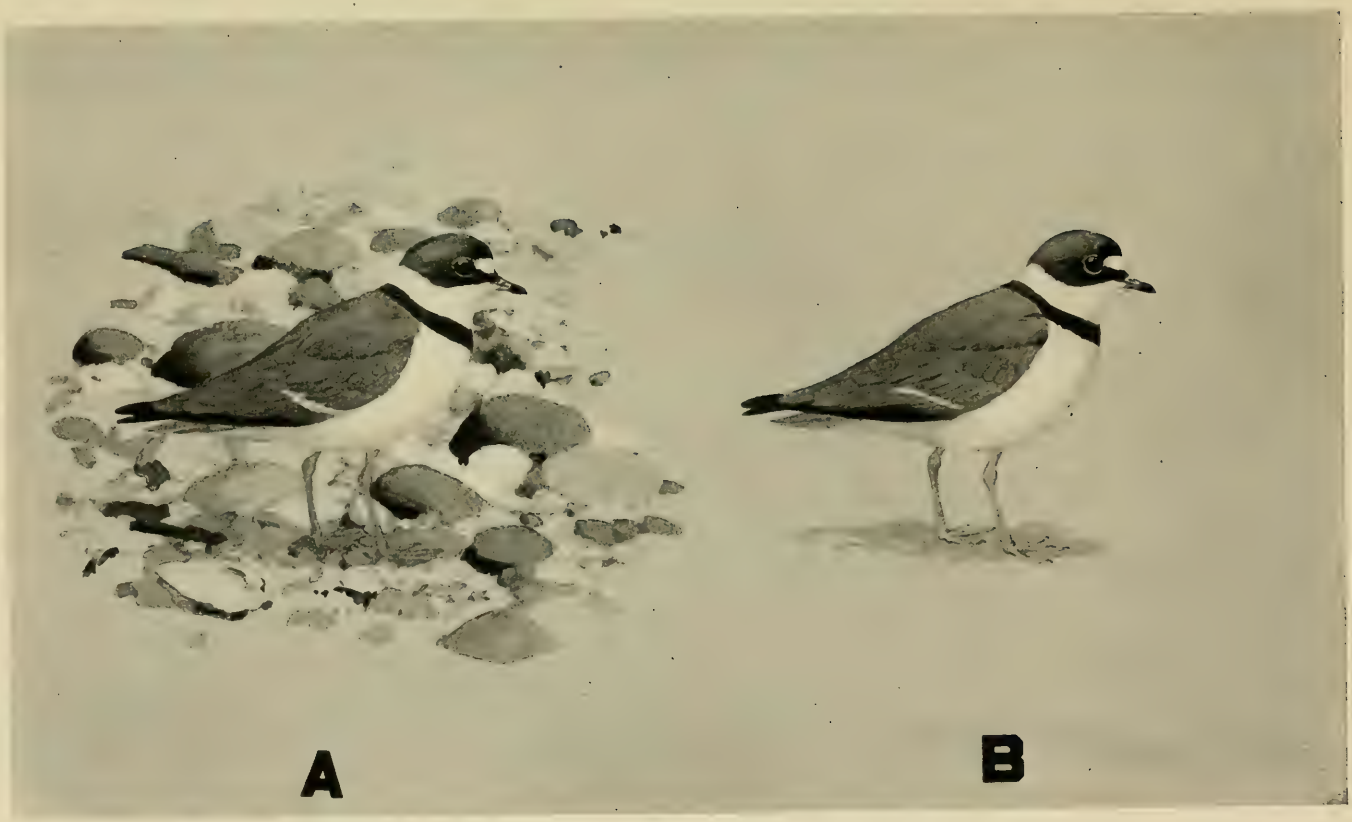
Many fishes, frogs, snakes, birds, and mammals have large rounded black pupils which conform to this very shape most likely to catch an observer's eye. However effectively such animals may be camouflaged in other respects, unless the eye receives special treatment, it will prejudice the success of the whole colour-scheme. It is therefore very interesting, though not surprising, to find that nature—the supreme camouflage artist—has dealt in great detail with this problem, which is evidently one of urgent importance. . . .

In its essentials, the method . . . invokes the optical principle of coincident disruptive coloration. . . . If an eye, and particularly its staring black pupil, can be made to appear another shape, then it will cease to resemble an eye. In theory, such an illusion could be created by covering the eye, or its pupil, with a black mask of irregular shape—so designed as to blend with and seem part of the pattern which surrounds it. Now that is essentially the system devised in nature. . . . Animals belonging to many widely separate families and orders have the eyes camouflaged in precise detail. Although the underlying principle is everywhere the same, the incidents of the picture vary widely in different cases. Sometimes an irregular dark disruptive area includes the whole orbit. Sometimes the upper margin of an elongated patch of dark pigment crosses the iris exactly on a level with the top of the pupil. Or conversely it may extend beneath to the pupil's lower limit. Or again the eye may be crossed by a stripe exactly the width of the pupil itself. In other cases similar effects are produced in vertical bars instead of horizontal stripes; or in diagonal markings or irregular shapes varying greatly in size and distribution. The one consistent feature in all this diversity is the significant relation between that unmitigated black spot—the pupil—and the dark element which serves to absorb it.

Given an animal with any or all of the types of concealing color pattern already discussed, it may yet be concealed in vain in some cases, if its contour or bounding margin be unaffected by the camouflage. Actually, in most cases of disruptive pattern the outlines of the animal are affected by it, and further marginal disruption is unnecessary, but in some instances the peripheral parts—tail, limbs, head and neck, or even the lateral contour margin are disruptively marked.

CONCEALMENT OF THE SHADOW

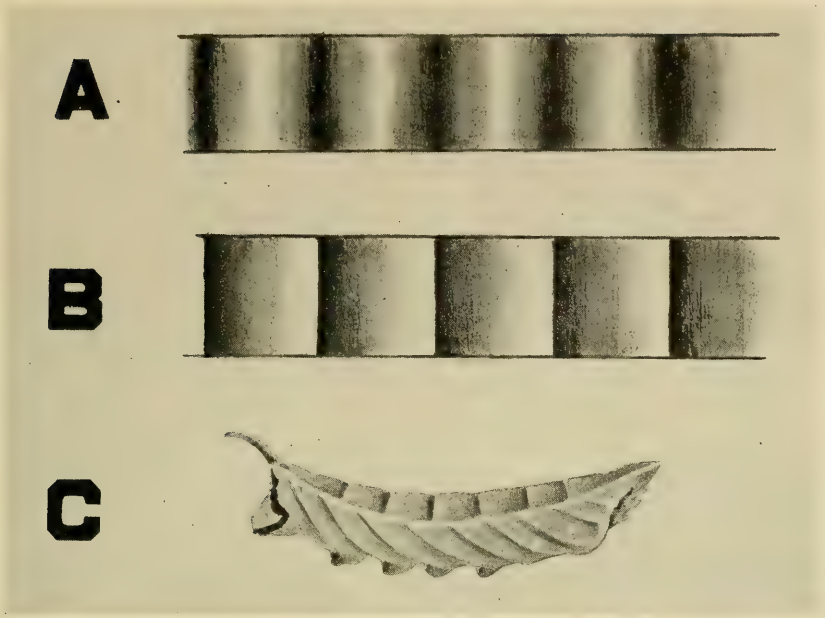
We have already seen, in the case of the white ptarmigan against a snowy background, that aside from the bird's lack of obliterative shading and its consequent visual solidity, its presence is revealed by the shadow it casts on the snow at its feet. In case of danger the shadow would be



THE EFFECT OF DISRUPTIVE MARKINGS IN THE RING-NECKED PLOVER (CHARADRIUS SEMIPALMATUS)

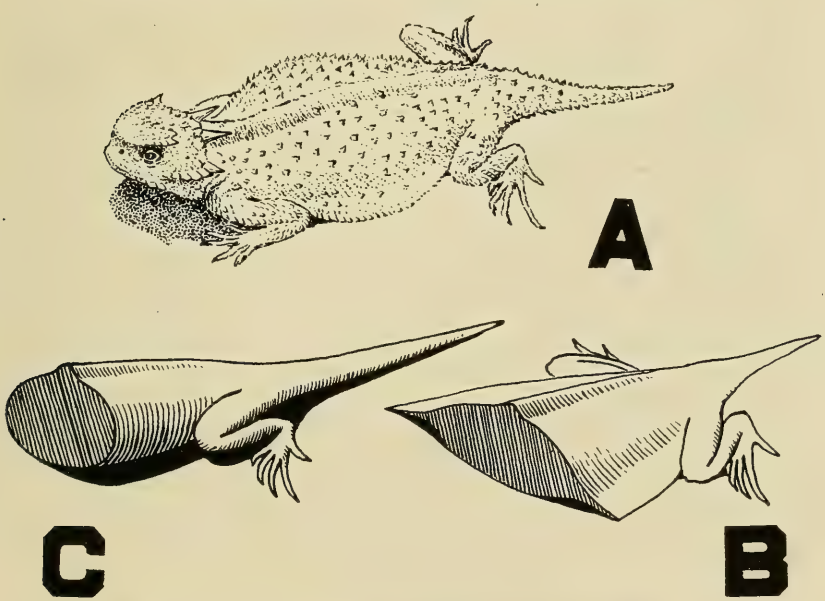
A, against its normal background; B, without its background. (Drawn by W. A. Weber.)

COINCIDENT DISRUPTIVE MARKINGS IN THE BRAZILIAN TREE FROG (HYLA NIGROMACULATA)
(Drawn by W. A. Weber.)



1. CONSTRUCTIVE SHADING

A, extreme dark and light tones connected by intermediate shading, giving a smoothly rounded appearance; B, extreme dark and light tones in contrasting juxtaposition, giving the effect of ridges; C, a leaf caterpillar (*Epistor gorgon*) with constructive shading giving the appearance of leaf vein ridges. (Drawn by W. A. Weber, after H. B. Cott.)

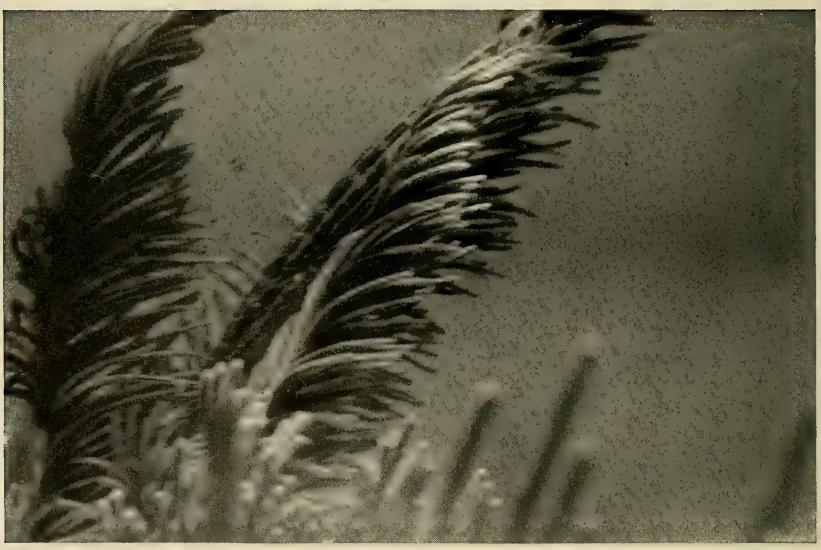


2. SHADOW ELIMINATION IN THE HORNED TOAD (PHRYNOSOMA CORNUTUM)

A, the animal as it appears; B, a diagrammatic cross section to show the lateral flanges covering the shadow; C, a diagrammatic cross section of what the animal would look like if it did not have the lateral flanges; note the revealing shadow. (Drawn by W. A. Weber.)

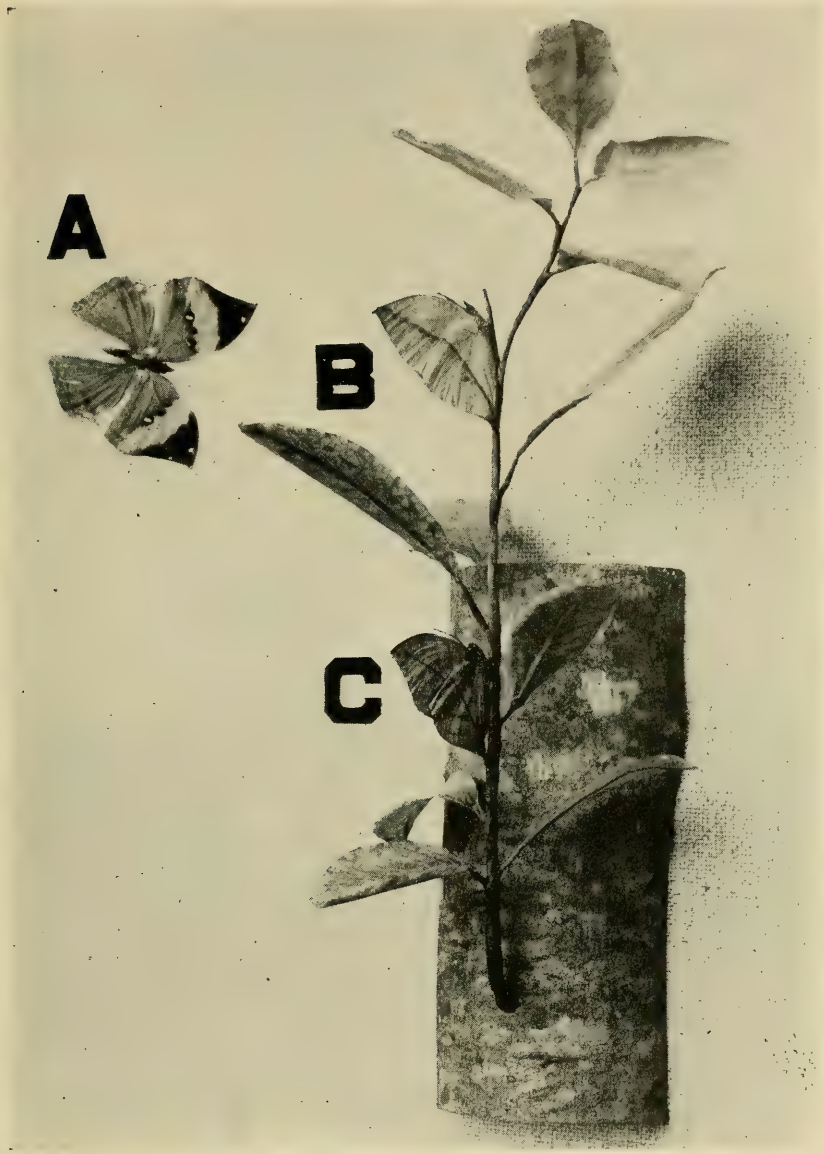
1. NEST OF WOOD PEWEE (MYIOCHANES VIRENS) SHOWING USE OF LICHEN FOR NEST CONCEALMENT

(From exhibit in U. S. National Museum.)



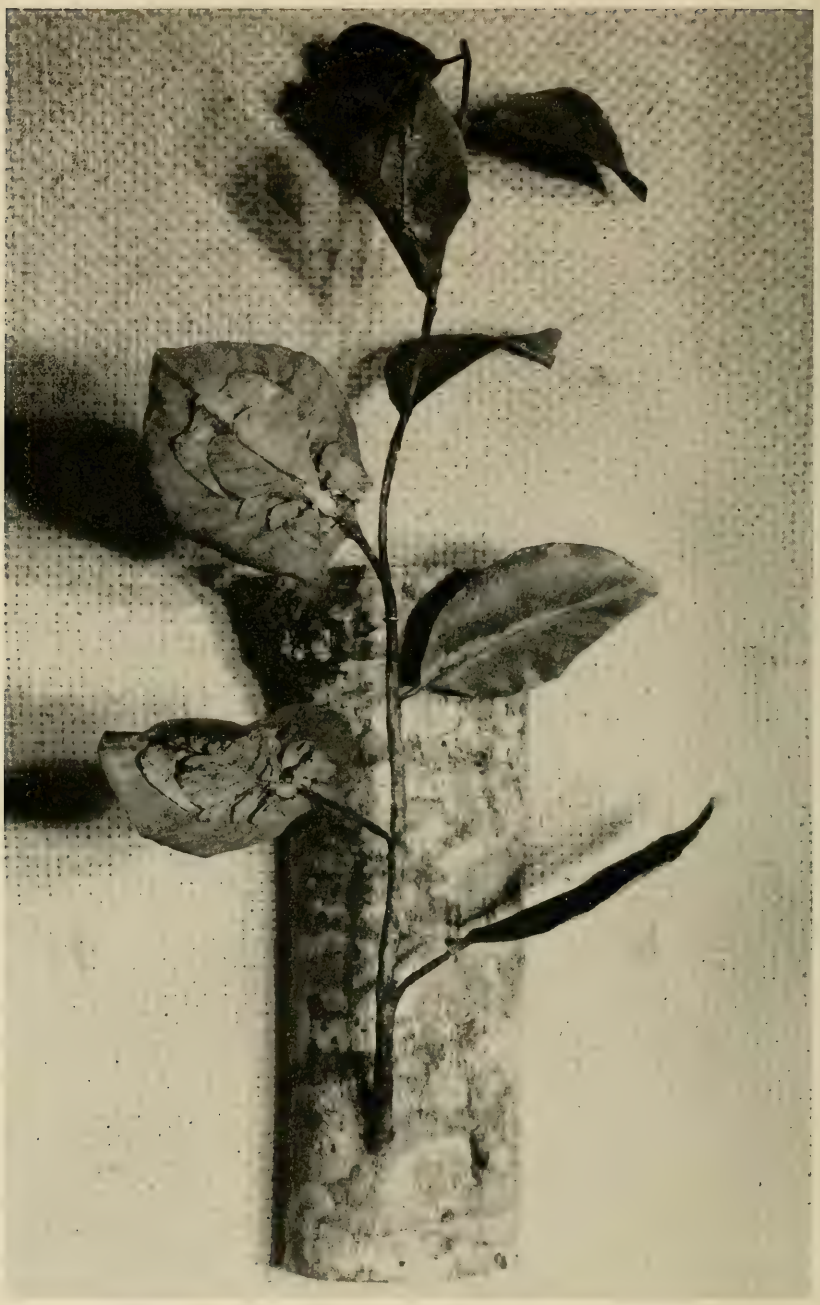
2. TRUMPET FISH (AULOSTOMUS MACULATUS) CONCEALED BY FORM AND COLOR-PATTERN RESEMBLANCE IN A SEA-FEATHER

(Photograph from Longley and Hildebrand, Carnegie Inst. Publ. 535, 1941.)



LEAF BUTTERFLY (KALLIMA PARALEKTA)

A, the butterfly in flight, showing the conspicuously marked upper surface of the wings; B and C, butterflies at rest, looking like the leaves around them. (From exhibit in the U. S. National Museum.)



LEAF INSECT, CHITONISCUS, SHOWING MORPHOLOGICAL AS WELL AS COLOR RESEMBLANCE TO THE LEAVES UPON WHICH IT FEEDS

(From exhibit in the U. S. National Museum.)

BARK-RESEMBLING INSECTS

(From exhibit in the U. S. National Museum.)

1. Walking-stick insects on twigs. (Photograph by H. S. Barber.)

2. Sargassum fish (*Pterophryne histrio*) in Sargassum weed.

FINE EXAMPLES OF CONCEALMENT BY BODY FORM

largely done away with, as the bird would squat low on the snow and actually cover a good part of its shadow. It is actually no exaggeration to say that in many cases of animals with a color pattern more or less concealing in nature, the shadow is more noticeable than is the animal casting it. In creatures of laterally compressed form such as butterflies that rest with the wings closed over the back, we find two definitely established orientation habits which appear to be related to the matter of shadow concealment or reduction. A number of species, notable among which is the green hairstreak butterfly (*Thecla rubi*), tilt the wings away from the median vertical plane toward the shadow, thereby hiding a large part of it. The degree of tilting is said to be constant for each species, and numerous independent observers have testified to the fact that the wing tilting is not a casual or accidental reaction, but is definitely correlated with the direction of sunlight and also to the approach of enemies. Another group, without the wing-tilting habit, always seem to orient the body with respect to the direction of sunlight when alighting on any object so that the shadow cast by the wings (which are the largest part of the creature) is reduced to a thin, inconspicuous line instead of a sizable dark area. In animals with dorsoventrally flattened or depressed body form, shadows are often reduced by the animal squatting closely against the ground or branch or whatever the creature is resting on, but in many cases there are structural features which, whatever their other functions may or may not be, do serve to reduce shadow by covering it from sight. Many reptiles and amphibians, such as the horned toad, have lateral finlike flanges on the tail which not only help to cover the shadow that would otherwise be visible, but by their gradual slope from the top of the tail to the substratum throw little if any shadow beyond themselves. These flanges make for unbroken continuity between the more substantial part of the animal and its immediate surroundings. The sides of the body are flattened out into longitudinal flanges. As we have already noted in discussing constructive shading, the effect of false shadows, such as those of the leaf vein ridges, may be brought about by pattern in some creatures, such as certain caterpillars.

DISAPPEARING COLORATION

All the items examined so far have to do with animals that are more or less stationary. There are also a great many animals that show bright patches or patterns when in motion but suddenly conceal them when alighting. From the standpoint of the pursuer it is very confusing to be chasing something with a bright, vivid telltale mark and then find it suddenly vanishing. It often results in the pursuer racing on beyond the

hiding prey and thereby losing all chance of securing it. Color patterns of this disappearing type are of two main kinds, the one depending on the distinctive pattern being actually covered when at rest, the other depending on differential orientation to light. In the first type the cases may be very simple, involving merely the disappearance of the bright color area, or they may involve elaborate protective color resemblance to the substratum on the part of the covering portions of the body. As may be expected, the second is far more effective as concealment than the first, but in both the element of confusing surprise is equally present. An example of simple disappearing coloration is the common North American woodpecker, the flicker (*Colaptes auratus*). In flight this bird shows a large conspicuous white patch on the rump, and bright golden yellow undersides on the wings and tail. On alighting these parts are immediately concealed, and an enemy following these beacons might well be confused by their sudden extinction. An example of the more elaborate type is the leaf butterfly (*Kallima paralekta*). This insect has a bright orange, brown, and whitish pattern of bold markings on the upper surface of its wings, which make it a conspicuous sight when the creature is flying. On alighting on a twig, however, the wings immediately close together over the back, leaving only their undersides visible. Both in color and in form the closed wings look amazingly like a dried leaf and the insect is suddenly completely concealed, to the bewilderment of its possible pursuer.

The other type of disappearing color is that found in animals with iridescent scales, feathers, etc. A gleaming ruby light, as on the throat of the male ruby-throated hummingbird (*Archilochus colubris*), is suddenly extinguished as the bird, in its darting about, alters its orientation to the sunlight. This is, in effect, disappearing coloration in motion, as opposed to concealment of color when at rest, and it may be argued that when in motion the creature is less in need of camouflage than when still, but within this lesser sphere of necessity, it may have a protective effect.

THE EFFECTIVENESS OF CONCEALING COLORATION IN NATURE

There has been much difference of opinion among naturalists as to the real effectiveness of concealing coloration in animals, some estimating its success as almost unbelievably complete, while others contend that it has no value whatever and is a reflection of a purely human approach to the subject. This paper is hardly the place to evaluate the arguments and the evidence pro and con, but it may be pointed out that the great majority of opinion does grant it some effectiveness, and, what

is even more important, animals that are what we call concealingly colored seem, by their habits, to rely on their coloration to save them from attack. It may be further mentioned that the application to man's war efforts of the principles involved in concealing coloration in nature have been generally conceded to be of sufficient effectiveness to warrant their continued and even increased use. We are not concerned in this brief review so much with the various details of the functions of concealing coloration as with a survey of the methods by which it is attained.

CONCEALING BODY FORM

Not only are many animals rendered less conspicuous by reason of their coloration, but also in many (and some of the most startling) cases by their form as well. We have already had a suggestion of this in the body and tail flanges that tend to eliminate or conceal shadow, but may now briefly consider some of the main types of disguise brought about by the shape and contours of the animals involved.

As might be expected, morphological (i.e., form) resemblances are to be found chiefly among smaller creatures whose whole lives are spent against unchanging backgrounds, i.e., creatures that are environmentally more rigidly fixed. Also, inasmuch as morphological resemblances are generally more specifically related to definite items in the surroundings than are many color resemblances (that are often of a general similarity to a background complex) it is to be expected that these special resemblances are chiefly to such things as leaves, bark, stems, seaweed, etc. On the whole, it may be said that the value of the various types of camouflaging coloration depends upon principles of visual concealment or confusion, while the morphological resemblances partake more of the nature of definite, specific, particulate disguises. For purposes of simplification, it may be said that we have to do here with the actual modeling of the body and not with constructive shading.

We have already seen an instance of leaf resemblance in the case of *Kallima,* the leaf butterfly. The ends of the wings are actually shaped like the stems of leaves and the outlines of the closed wings are duplicates of the periphery of leaves. Even more elaborately worked out is the leaf resemblance of not only the whole, but even the parts of such leaf insects as *Chitomiscus* and *Cycloptera.* Aside from the all-important details which make or mar the effectiveness of the disguise, the basic common element in all leaf-resembling creatures is thinness. Whether the thinness is produced by a dorsoventral flattening or depression of the body or by a lateral compression, the creature orients itself accordingly with respect to its background, just as we found in the types of shadow elimination in

butterflies. Leaf resemblance is found not only in insects, but also in some fishes, chameleons, and other forms of animals.

Resemblance to bark is one of the commonest types of morphological disguise. The reason for this is that all barks (in spite of definite specific differences) show a smaller range of variation than do all leaves, for example, and at the same time the bark fauna is very extensive. Bark-resembling creatures include many moths, beetles, spiders, tree frogs, climbing lizards, and a few birds. In the moths alone, many distinct families have produced instance after instance of bark resemblance.

Closely connected with bark resemblance is resemblance to lichen, as lichen is so frequently found on places analogous to tree trunks (from the standpoint of their inhabitants). Not only do we find the same range of animals in all parts of the world with lichenlike appearances or with strong bark resemblances, but we even find animals using lichen apparently for their concealing properties. For example, the ruby-throated hummingbird (*Archilochus colubris*), the wood-pewee (*Myiochanes virens*) and the blue-gray gnatcatcher (*Polioptila caerulea*) cover the outsides of their nests with lichens, with the result that they are very well concealed.

Also associated with bark resemblance are those cases of twig resemblance, well illustrated by the familiar walking-stick insect. All parts of the body are here modified into slender twiglike pieces, and the joints between them have much of the appearance of plant nodes. Furthermore, the postures struck by the insects are in keeping with the illusion of small twigs. As a matter of fact, the harmony between usual posture (which is not rigidly fixed in most cases) and the illusory form or color resemblance in many of these concealing-colored animals is one of the strongest lines of evidence for the reality of the camouflage. Otherwise, it might well be a purely man-made interpretation, but when creatures seem to act according to this color or form, or to be colored and shaped according to their normal activities, it is difficult not to grant the reality of this correlation.

In the sea we find crustaceans and fishes that have many irregular filamentous appendages, which bring about an astonishing resemblance to the seaweed in which these particular species live. The fauna of the Sargasso Sea, an area in the Atlantic Ocean filled with the Sargassum weed, are perhaps the best-known examples of this kind, although others occur in all the oceans wherever seaweeds are common. There are numbers of species of small fishes, of crabs, etc., that spend their lives in the floating masses of Sargassum weed, and of this ecologically closely limited fauna, the percentage of seaweed form resemblance is high indeed. Speci-

mens taken out of their natural environment seem merely bizarre curios of the naturalists' cabinet, but in their native haunts they merge completely into their surroundings.

CONCLUSION

Camouflage in nature is, then, widespread, both in all parts of the world, and within all groups of animals. It may be brought about by coloration alone, by form alone, or by any possible degree and type of combination of color or morphological characters. It may be rigidly fixed or remarkably plastic. Its degree of success in different forms is highly variable, and, as might be expected, the opinions of investigators as to its merits have been equally diverse. In this brief review we have merely pointed out some of the types of camouflage, have given some idea of its complexity, of its multiplicity of methods and approaches, and of the astonishing heights of deceptive efficiency it attains in many cases. Such controversial outgrowths of the subject as mimicry and the theoretical difficulties it entails have been deliberately left out of the present discussion.

39088000965806